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The Course and Growth of the Fibro-Vascular Bundles in Palms. By John Casper Branner, B. S.

(Read before the American Philosophical Society, October 19, 1883.)

The classification of phænogamous plants as endogens and exogens was based upon the theory of the supposed course and development of the fibro-vascular bundles in the stem of the palm. That a question of so much importance botanically has received no more careful attention, is probably due to the fact that the original theory of endogenous growth was considered so simple, satisfactory, and self-evident from a transection of a palm trunk, that its very simplicity was an impediment to investigation.

Comparatively few botanists have given especial attention to the subject of the structure of the palm stem, and those who have done so, have encountered so many difficulties in obtaining proper material,* and in getting satisfactory results from material to be had, that our certain knowledge upon the origin and course of the fibro-vascular bundles is still confused, and the theories and explanations of growth unsatisfactory and even perplexing. The best observers failed to grasp the whole subject, while others have given us masses of useless, irrelevant, and erroneous matter with only here and there a useful fact. From such results it is so difficult to select that which is useful, that it is simpler to leave the whole to one side and do the work all over from the beginning.

The difficulty, almost impossibility, of tracing the course of the fibro-vascular bundles in the hard, complex palm stem, has added not a little to the uncertainty and doubt that every one has felt who has advanced a theory of growth, or tried to prove their direction by actual dissection.

The peculiar structure of the trunk of the palm was mentioned about 300 B. C., by Theophrastus in his Historia Plantarum, Bk. I., Chap. IX. In the sixteenth century, Rumphius, French Consul on the Dutch Island of Amboyna, called attention to the same point, and in the seventeenth century his observations were confirmed by those of P. Labat, in the West Indies, and also by those of Desfontaines, made in Tunis and Algiers.

As a botanical question it may be said to have been opened by Desfontaines, member of the French Academy of Sciences, who, while he propounded a theory, personally took very little part in the discussion he had raised.† A general statement of his theory given by Mirbel‡ is sufficient for present purposes. In the "Fragment d'un voyage dans les Régences de Tunis et d'Alger, fait de 1783 à 1786," p. 290, Desfontaines says: "La

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* Mirbel went to Africa to study the structure of the date palm, but even there found it almost impossible to obtain a grown one, and was about to abandon his work when a gentleman gave him a specimen.

† His views were published in the "Mémoires de l'Institut National," Vol I., 1798, pp. 478–502.

‡ Comptes Rendus de l'Académie des Sciences, 1843, Vol. I., June 12.

moelle des Dattiers est placées dans l'interval des fibres qui vont toujours en se serrant du centre à la circonférence, en sens contraire des autres arbres, et elles ne sont pas placées par couches comme j'ai en mille fois l'occasion de l'observer sur des troncs coupées."

Although Desfontaines kept comparatively quiet upon the subject, pupils of his, and especially Daubenton, took up his theory, and did all in their power to give it general acceptance in the scientific world. We know how successful they were, for, in 1819, de Candolle published the classification in which all phænogamous plants were divided into endogens and exogens. This classification was based upon the theory of Desfontaines, and, after its publication, was accepted without question of importance up to 1824, when Hugo von Mohl published his "De Structura Palmarum." Previous to Von Mohl, however, Moldenhawer had denied the theory of Desfontaines. As stated by Mirbel,* this theory of Moldenhawer was, that the fibro vascular bundles in monocotyledons take the place of the woody layer in dicotyledons, and that the lignification begins at the centre, and gradually approaches the circumference. If Mirbel's be a true statement of Moldenhawer's theory, I see no reason for considering it of much importance, as it was only proposing to replace one error by another.

The next work upon palm structure is that of Hugo von Mohl, published in 1824, as an introduction to Dr. C. F. P. von Martius' "Genera et Species Palmarum."† Von Mohl's work was done so carefully and conscientiously that although his theories have been attacked, and more or less modified by Meneghini and Mirbel, they have been generally and justly accepted as the best, if not the true ones, up to the present time. And, however much one may disagree with Von Mohl's conclusions, he cannot help feeling that his work would have been more thorough and more satisfactory if he had had more extended opportunities for observation. He admits that he had only young specimens, and portions of full-grown palms to work upon,‡ and any one who has tried to investigate this subject, can appreciate the difficulty or impossibility of demonstrating anything satisfactorily in a short section of a mature trunk, and may well wonder that Von Mohl came so near the truth with such unsatisfactory material from which to gather his facts and draw his conclusions. Writers upon palm structure are continually referring to the difficulty of dissection and investigation, and in the literature of the subject we find them admitting their inability to make out certain points§ on account of the impossibility of following the bundles.

Next after Von Mohl came Meneghini in his "Recherche sulla Struttura," etc.,‖ published in 1836, and followed in 1843 by more recent observations, under the title of "Intorno alla Struttura," etc.‖

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*Comptes Rendus de l'Acad. des Sci., 1843, Vol. I., p. 1216.

†See under Von Mohl in literature at end.

‡V. Ray Society, 1849, pp. 73-77.

§Ray Society, 1849, p. 85.

‖V. literature at end, under Meneghini.

In 1839 the French Academy of Sciences sent out one of its members, M. C. F. B. Mirbel, to Africa for the purpose of investigating the structure and manner of development of the date palm, and in 1843 the results ot Mirbel's work were given to the Academy.* The following year Mirbel contributed a paper on the structure of *Dracæna australis*, in which he also referred to the question of palm structure.† Contributions to the subject were made by Lestiboudois‡ in 1840, and by Unger§ in the same year.

In 1845 Dr. C. F. P. Von Martius gave a statement of his theories upon the subject.‖ Sachs, in his text-book¶ refers to Nägeli,** and Millardet** as authorities upon the direction of the fibro-vascular bundles, but there is nothing in his own explanations to lead one to suppose that these writers differed materially from Von Mohl.

These are the names of the principal contributors to the literature, and since Von Mohl published his appendix in reply to Mirbel and Meneghini in 1845, it will be seen that little or nothing has been done in the way of original investigation.††

I will now briefly restate the theories held by the principal investigators in regard to the more important characters of palm structure.

First, we have the theory of Desfontaines, Daubenton and de Candolle, which prevailed up to 1824, and which has scarcely yet been completely eradicated from text-books on botany.‡‡ This was the theory of endogenous or inward growth. It held that the inner fibro-vascular bundles in a palm trunk ran to the new fronds, and the outer ones to the old. This theory was probably largely due to the fact, that in a transection of a palm trunk the outer bundles are hard and bony, while the inner ones are tender, and generally of a lighter color. Considering the state of botanical knowledge at the time this theory originated, it was perhaps a natural conclusion to draw from so limited an investigation of the subject. A hemisection of a palm trunk, as they understood it, would be represented diagrammatically by fig. I., and a transection by fig. II. Fig. II. has the fibro-vascular bundles displayed just as we find them in fact, the softer and lighter-colored ones through the centre, and the hard bony ones next the periphery. This crowded condition of the outer bundles was supposed to be the result of the growth of the new bundles at the top of the trunk, which pressed them out, and packed them closely together. This was also supposed to account for the even size of palm trunks.

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* Comptes Rendus de l'Acad., 1843, Vol. I., p. 1213.

† Comptes Rendus de l'Acad., 1844, Vol. II., p. 689.

‡ "Études sur l'Anatomie et le Physiologie des Végétaux."

§ "Ueber den Bau und das Wachstum des Dicotyledonstammes," 1840, p. 35.

‖ Comptes Rendus de l'Acad., 1845, Vol. I., p. 1033.

¶ Oxford ed., 1875, p. 552.

** V. literature at end.

†† Dr. Gray refers (Text-Book, 6th ed., 1879, p. 71, foot note) to a memoir of recent date by Guilland: "Recherches sur l'Anatomie Comparée et le Developpement des Tissus de la Tige dans les Monocotyledones." Ann. Sci. Nat., Ser. 6, V., 1–176, 1877. I have not seen this work.

‡‡ Dr. Gray says that the word "endogenous" is still retained for the purpose of indicating a peculiar stem structure.

The theory of Von Mohl, based upon careful study, completely overthrew the theory of Desfontaines. His investigations showed too that the structure of the palm trunk was no such simple matter as had been supposed. The leading features of Von Mohl's theory are as follows : Dissecting out a fibro-vascular bundle from the base of a frond, it curves in to the centre of the stem, and downwards, and after a short course through the centre of the trunk gradually approaches the periphery, and then runs down into the base. Later Von Mohl modified this statement, recognizing the fact that his investigations had been made upon too young specimens, and that in a full grown stem the bundles did not reach the base.* He then concluded that their lower extremities ended blindly on the periphery, and that at their upper ends they grew into the phylophore.† He observed their difference of structure in different parts, their varying size, their hardening, coloring, the slight growth in size of the bundles blending, and, after it was called to his mind by Meneghini, recognized their spiral direction (though he attached no importance to it‡), and that the course of the fibro-vascular bundles was the same in all palms.

Meneghini laid stress upon the oblique course of the bundles, and explained it as a mechanical result of unequal growth of stem and frond scars. He supposed the trunk to outgrow the leaf so much that the base of the frond was thrown out of its former relation to the other fronds, and that the bundles were thus drawn to one side, causing this obliquity in their direction. The occurrence of fronds at the same angle to each other on the stem was accounted for in the following manner : In the apex, as he believed, the fronds were arranged in a helix, which, in the course of growth, became a spiral line upon the stem, the fronds all having been drawn aside equally. He also advanced a theory of the creation of the fibro-vascular bundles by currents of sap in the phylophore, and thought they were to "be regarded as descending from the nascent leaf in the centre of the bud." §

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*Duchartre, in his "Éléments de Botanique," p. 179, gives Von Mohl's theory in its original form, and in a figure represents the fibro-vascular bundles as all running into the base.

† There has been no little misunderstanding of Von Mohl's theory and descriptions. Mirbel did not know whether he meant that the bundles grew downwards from the bases of the fronds (Comptes Rendus, 1843, p. 1218, *et seq.*). In stating Von Mohl's theory, he says that "selon M. Mohl, les filets * * * * * partent des feuilles," and a little further on he declares that he does not know what Von Mohl means by saying that "les filets partent des feuilles et descendent vers la base."

Duchartre in his "Éléments de Botanique," p. 177, in explaining Von Mohl's theory, says of a fibro-vascular bundle: "Il descend verticalement sur une certaine longueur."

‡ Duchartre has credited Von Mohl with the discovery of the spiral direction of the bundles ("Éléments de Botanique," p. 177), but Von Mohl confesses that he laid no stress upon it, leaving us to infer that he had observed it. Ray Society, 1849, p. 52, third line from bottom.

§ Ray Society, 1849, p. 90.

Mirbel stated that the fibro-vascular bundle originated in a utricle at the periphery of the phylophore, and grew upwards into it, whence it curved outwards and entered a frond base on the side opposite the one upon which it originated.* "Le plus grand nombre, si n'est pas la totalité, nait à la surface interne du phylophore * * * * une partie d'entre eux s'allongent et monte à peu de distance de cette surface, puis se courbe tout à coup vers la périphérie et va joindre la base des feuilles, qui elles rencontre *chemin faisant.*" He believed the number of bundles in a stem might increase indefinitely, and in this way he accounts for the spindle-shaped trunks of certain palms.

Gaudichaud's theory was, that the bundles all originated at the frond bases† in the phylophore, and grew downwards to the base, and out to the ends of the roots. Says M. Gaudichaud :‡ "M. Mirbel soutent que c'est de bas en haut qu'elle agit ; moi je prouve par des faits, par tous ceux que j'ai observés que c'est de haut en bas, des bourgeons aux racines * * * Ils marchent donc !"

At the close of the reading of his seventh and last paper on this subject before the French Academy, he says, that whatever the Academy may think about the matter "il ne me restera plus qu'à m'écrire, moi aussi : Et pourtant ils descendent !"§

Dr. Von Martius stated,‖ that all fibro-vascular bundles connected with fronds ; that they originated in the phylophore, exterior to and below the others ; that the points of origin were organic ; and that they grew upwards and downwards. He believed the bundles to end blindly below in the periphery, and that they might come to the surface above, either on the same side of the stem, or on the side opposite.

It is not my purpose to offer just here the objections that might be raised to the theories of these different authorities, but to present the result of my own observations in order, and to point out wherein they differ materially from those of others.

A transection of a full-grown palm trunk shows a number of hard fibro-vascular bundles scattered through it, without any further arrangement than that they are more numerous, harder, and generally colored near the circumference, while the parenchymous or pithy part prevails in the centre. A hemisection from base to apex shows (Figs. III, IV,) that the bundles have, for the most part, the appearance of being parallel, while at short intervals a few of them are seen to curve out from the centre of the stem to the fronds, or to the spadices growing in the axes of the fronds, or in case both spadices and fronds have fallen, to their old scars.

In trying to trace any one of these bundles, we find that it, sooner or later, becomes entangled in the mass, or that it has been cut across in making the section. With a hard stem this is invariably the result, but if the stem be a decayed one, in which the cellular tissue has disintegrated and left the bundles more or less free, the direction of a bundle may be followed with more or less certainty. Beginning with one of these where it curves inward and downward from the base of a frond, it may be traced inward to or near the centre, then downward, gradually approaching the circumference again. In this lower part of the bundle, however, the angle of divergence from a parallel with axis and periphery is so small in most palms, and the little curves made by the bundle in crossing others so misleading and confusing, that it is with some difficulty one can appreciate the fact that the bundles are not all parallel to each other and to the axis of the stem. If, however, the internodes are short, and the trunk is comparatively large, we may expect to find this angle more defined. This is very marked in the rhizomes of the so called trunkless palms* upon which the fronds are crowded in the shortest possible length of trunk. In these rhizomes this direction of the lower extremity of a division of a fibro-vascular bundle is visible at a glance. On approaching the periphery of the trunk the bundle is found to decrease in size, and finally it breaks off and appears to end blindly in the mass of other bundles near the surface. As far as can be made out then, in a full grown stem, by this method of dissection, this is what we find the course of the fibro-vascular bundles to be : from the base of the frond they curve sharply inwards to the centre, and then gradually outward to the surface, and there end. If it were possible to take up the bundles in any part of a stem, and follow them *upwards*, one after another, it would be found that they all connect, sooner or later, with fronds or spadices† (or their scars), and that none of them end blindly on the internodes.‡

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* Comptes Rendus de l'Acad., 1844, Vol. II., p. 690.

† Comptes Rendus de l'Acad., 1845, Vol. II., p. 264.

‡ Loc. cit.

§ Loc. cit., p. 272.

‖ Comptes Rendus de l'Acad., 1845, Vol. II., p. 1038.

So far I have spoken of tracing a bundle downward from the insertion of the frond. To this method of dissection is largely due the uncertainty about the lower extremity of a division. By examining the apex, or growing part of the trunk, it may be seen that these bundles do not end blindly at their lower extremities upon the surface of the stem, but that they are connected in sections or divisions§ from the base to the apex, one with another, and one on top of another.

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* In classifying palm stems according to their structure, Von Mohl made a sub-division of the rhizomes of trunkless palms, but made no investigation of them on account of lack of material. V. Ray Soc., 1849, pp. 6-7.

† Dr. Von Martius does not mention bundles connecting with spadices.

‡ In his "Text-book on Botany" (Ed. of 1879), Dr. Gray gives a figure of a palm trunk which represents the fibro-vascular bundles coming to the surface very much at random, and bending outward all through the stem. This is not what is seen in a palm stem, especially if the internodes are of any considerable length, but the bundles turn out to the fronds or scars *only*, and never to internodes.

§ I have spoken of the parts of a bundle between the points of branching as *divisions*.

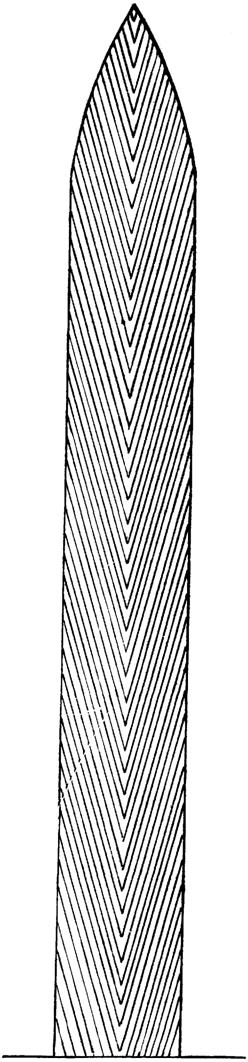


Fig. I.

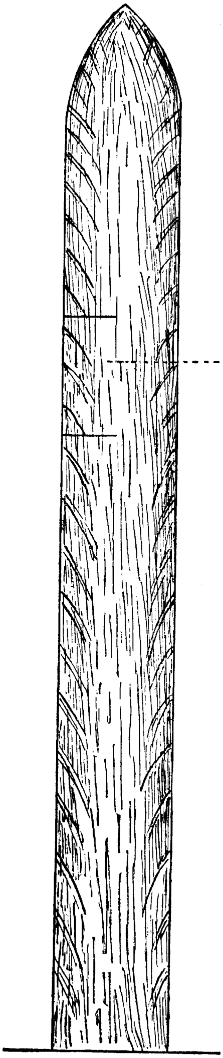
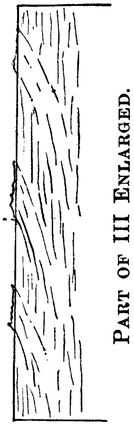


Fig. III.



Part of III Enlarged.

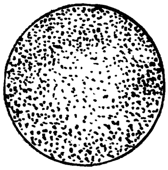


Fig. II.

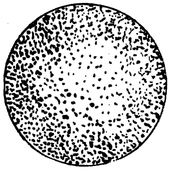


Fig. IV.

I will first show how these divisions came about, and then show how this effects the whole system of structure. From the points of connection with the fronds or spadices, the fibro-vascular bundles branch, one part having the immediate external growth (either frond or spadix), developed in connection with it, and the other continuing to form part of the stem proper above this point.* It will be seen later that these divisions of the bundles reach their greatest developement within the stem just at this point of branching. Whether it is on this account, or for some other reason, whenever a bundle has a frond developed in connection with it, the development of the stem branch is retarded. The attenuation of the lower extremity of a division, consequent upon this retarded development, renders it impossible, in most cases, to trace out the connection between the divisions, however carefully one may work. The elimination of the harder part of the bundle renders the observation of the connection still more difficult and uncertain.† In cases where this connection has been observed, it has been mistaken for blending, ‡ which often occurs, but which is quite another matter. Blending may take place in any part of a bundle's course, and may be in almost any direction, while the branching I here refer to, always takes place somewhere between the point where the bundle is tangent to a line parallel with the axis of the stem, and the point of insertion of the frond, and is always in the direction of the apex of the trunk. Blending may be upwards or downwards or sidewise, and may take place in any part of the whole length of the stem. It is often observable that just above the point of branching another bundle is developed on the inner side of the main division, but this piece is not continued as a distinct bundle, but as a part of the principal one.

Beginning then at the base of a palm trunk, a bundle is traceable into a frond. at the base of which it branches ; the stem division gradually approaches the centre of the stem, and there curves sharply outward to connect with another frond, and so, curving in and out, it connects with frond scars and spadices from base to apex.

Let us now consider these two directions of the fibro-vascular bundles : the gradual approach toward the centre of the trunk above the point of branching, and the comparatively sharp curve outward to connect with the external growth.

Why does a bundle always return to the centre of the stem, instead of going in a straight line from one scar to another?

First : the development of a fibro-vascular bundle is always in the

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*The connection between the divisions is seldom easily found, some species show it much more plainly than others. The specimens in which I have seen it most often and most distinctly were of *Raphia tœdigera*.

† Von Mohl admits his inability to determine how these small bundles ended below. Ray Society, 1849, p. 69.

Duchartre ("Éléments de Botanique," p. 179) says: "Il se réduit à l'état de filament délie à son extremité inferieure."

‡ Blending is mentioned by Lestiboudois (V. Literature at end), by Unger, and by Von Mohl. Ray Society, 1849, p. 8.

direction of the apex of the phylophore. When in the process of development, a bundle has a frond or spadix formed in connection with it, it is clear that the base of this frond, being left behind by the growth of stem and bundle, must at some time become a scar upon the side of the stem, and as the developing point of the bundle is always near the apex, the bundle will be formed more or less in a line connecting the scar or point of branching and the apex of the phylophore which is in the axis of the stem. But although the bundle is formed in this line, it does not follow that on the growth of the trunk it will be found in a straight line from the scar to the apex. In reality we find the lower extremity of the division as nearly as may be parallel to, and very near the side of the stem. This will be better understood from figs. V, VI and VII.

Let C be the apex of the phylophore at which a bundle branches. In the process of growth of the phylophore, the point C will be left behind at D, and the growing division of the bundle, pointing always toward the centre, will be developed in the direction DC or JI, practically very nearly parallel with the side CHD. Now when the apex is far beyond the original point of branching of this bundle, say at A, while the original point of C is at B, this part of the bundle that was formed first after the branching took place, will still have its original relation to the side of the stem, that is, it will be about parallel to it. When the point C is left at E, the direction will be still further changed, and will be IK, farther from the periphery, and when IK is left far behind it will be in a position like MN in figure V. Then again when the point C is left at B (Fig. V) we shall have the part IL forming, and thus will the growth of the bundle in length gradually approach it to the axis of the stem. Upon its arrival at a sufficiently advanced stage of development to take its place again, and again have a frond developed in connection with it, it will have crossed in its course all the bundles that have branched since it branched at C originally. I would suggest that this development of the fibro-vascular bundles, always in the direction of the apex, is due to the light. This apex, at its central point, is very pulpy and translucent, while its sides are enveloped by the young and growing fronds, which render the parts surrounding the centre more or less opaque.

The outward curve of these bundles is a simple matter. It marks the line traversed by the base of the frond from the time it originated at the apex of the phylophore until it reached its place on the side of the trunk. In figure VIII, let C be the centre of the growing part at which the frond and bundle connect. Now when the apex has grown to C', the point C will have been left behind at A upon the side of the growing cone, and when the apex is at C'''', the point which was originally at C will have taken its place at E upon the side of the stem. In this outward curve, the longitudinal growth of the bundle is shown. In figure IX if C be the former position of the apex at which a frond was developed, and which takes its place later upon the surface of the stem at D, it might be inferred that CF were the vertical distance grown by this section of the stem from the time the frond originated at C until it reached D. But such is not the case, for some allowance must be made for the increase of altitude caused by the side CG becoming parallel with the lower part of the stem. Taking GC as a radius and describing CI, the distance IE must be deducted as this difference in altitude of the point C when it reaches I, and the length grown by the whole section is FL or DI. It is true that when C reaches D, CF will be the difference in altitude made by C, but this is not all due to the growth in the length of the fibro-vascular bundles. In actual hemisections of palm stems it is noticeable that the curve CD is not an even one, but has a shorter radius near the point D. This is due to the fact that during the younger stages growth was principally in length, while as the part approached maturity, the lengthening was less marked, and the lateral growth predominated. This growing in size after prolongation has ceased is a characteristic of the fibro-vascular bundles in the palms. In the phylophore, the lengthening of the bundles is still possible to a limited extent, but it will be shown later that the growth in size continues even below the phylophore. It will also be seen later that this increase in the size of the bundles, and consequently in that of the whole stem after longitudinal growth has ceased, causes the fronds to droop more.

It has already been observed that the fronds are developed in connection with the *central* bundles in the phylophore. In regard to the origin of the bundles it is sufficient at present to say that they originate at the apex of the phylophore, and are developed in it, with it, and as a part of it. Von Mohl and Mirbel maintain that these bundles grow up into the phylophore; Gaudichaud that they grow downwards from it—from the frond bases; Von Martius that they grow both up and down, while I maintain that they are perfected in all directions at the same time, though the lateral growth continues to a certain extent after the longitudinal growth has ceased, and that they can no more be said to grow upwards or downwards than can it be said of the bones of the body that they grow outwards into the limbs. It is true that the general lengthening of the bundles takes place at the superior end, but there is a growth beside this. At the first appearance of the fronds at the apex of the phylophore the fibro-vascular bundles are already connected with them, and just as intimately as they are in the perfectly developed frond. The internodes at this point are very short, but the bundles are the same in number, and have exactly the same connections, directions, and relations to each other that they have in later life. But in the perfected frond we find them larger, longer and harder, and in the perfect stem the internodes are longer, the stem and bundles larger, while the whole plant has grown both longitudinally and laterally. In view of this general growth, the relations of the parts remaining the same, it is clear that growth does take place in all directions. In figure IX, p. 471, the upward and downward growth of a bundle is represented approximately by the line CD. This line cannot be upward growth alone, for the point D was once at C,

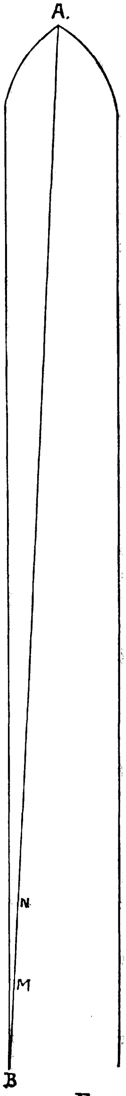

Fig. V.

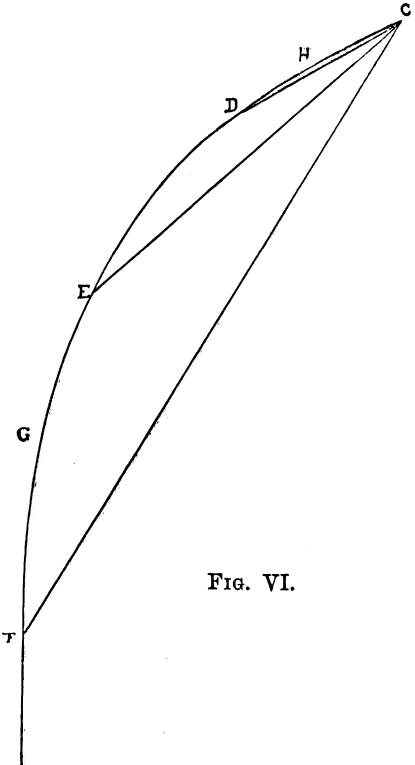

Fig. VI.

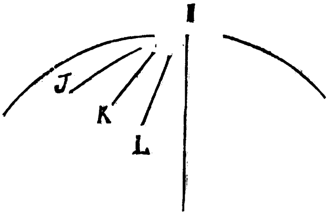

Fig. VII.

and when there, was a point on the surface of the phylophore. Now it has become a point on the surface of the trunk, the distance CD beyond its original position. so that the whole bundle must have grown in this part.

The theory of downward growth from the frond to the base, as held by M. Charles Gaudichaud, appears to me, as it did to Von Mohl,* unworthy of serious consideration. Mirbel's theory of upward growth of the fibro-vascular bundles was denounced by M. Gaudichaud as a physiological impossibility ; and it might be said of M. Gaudichaud's theory, that downward growth, as held by him, is a mechanical impossibility. From the course of the bundles, as already explained, it is seen that to grow downward, they would have to pass through the bony outer layer of the trunk twice : once on entering it, and again on approaching the surface lower down. Moreover the bundles at the base of the trunk would either have to be extremely small, or the base itself very large, neither of which is the case. It will be seen later, also, that the lower extremity of a bundle division hardens first, thus precluding all possible growth.

The reason that the fronds are always developed in connection with the central bundles, is because the central bundles are the ones there present, and the ones in the most advanced stage of development. It has already been noticed that when a frond is developed and a bundle branches, the part in connection with the frond is developed rapidly and at the expense of the part leading upwards. Having its development thus retarded, and being carried to one side by the growth of the trunk, this ascending division is attenuated at its lower extremity. Other bundles gain upon it in point of development, and take its place at the centre of the growing part. But in the course of time this division regains its vigor, and its place at the centre of the phylophore, where it is again the most advanced in development, and again has a frond or spadix formed in connection with its branches, and is again curved outward.

At the time of branching the formation of the frond is the immediate object of the bundle, but provision is at the same time made for other fronds higher up.

The branching goes on from the base of the trunk to its apex, varying only as the tree becomes old, and its vital powers diminish, the result of which is shorter internodes, and consequently shorter divisions of the fibro-vascular bundles.

The number of bundles may be said to be the same in all parts of the stem, and it is to this fact, taken in connection with the average even size of the bundles themselves, that the equal size of the palm trunk must be attributed. In specimens of which I have estimated the number of bundles at different altitudes, there has generally been a difference in favor of the base of the stem, but this difference is so slight that I believe the decreased vitality of the plant is sufficient to account for it. It is also

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* Ray Society, 1849, p. 52.

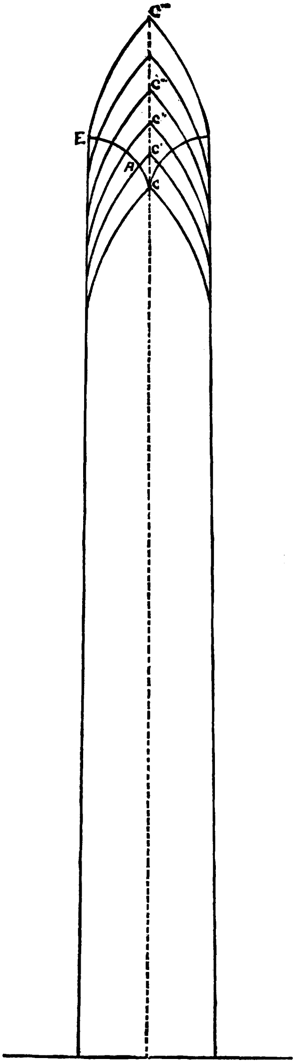

FIG. VIII.

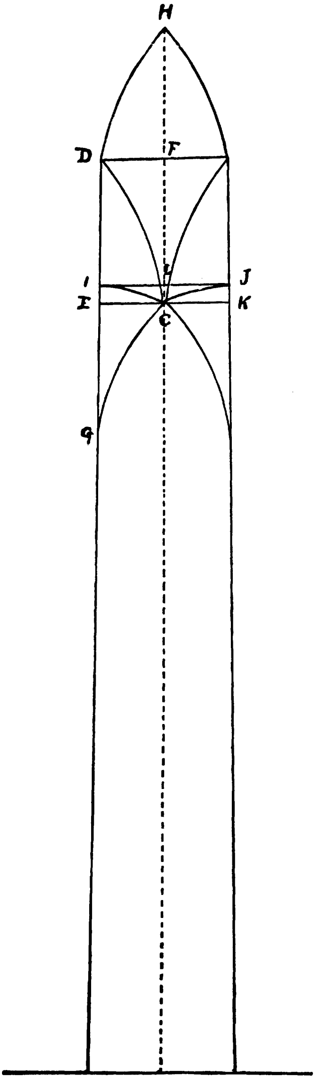

FIG. IX.

possible that the same number of bundles was present in the upper sections as in the lower ones, but that being smaller, they escaped my attention. In this connection I will refer to Mirbel's explanation of the spindle-shape of the stems of *Iriartea ventricosa* and *Acrocomia lasiopatha.* Referring to Von Mohl's theory, as originally stated, that all bundles ended in the base, M. Mirbel said :* "Il est un fait dont sans doute M. Mohl a connaisance, c'est qu'il existe des Palmiers pourvus d'un stipe mince à la base, mince au sommet et notablement renflée dans sa partie moyenne. Ce stipe resemble donc a une enorme fuseau * * * * * Je demande a M. Mohl comment il explique cette anomalie en restant fidèle a son hypothèse. Pour moi, rien de plus simple depuis que j'ai reconnu dans le Dattier que les filets naissent de bas en haut, de tout le pourtour interne du stipe, et à toutes les hauteurs. A la naissance de l'arbre fusiforme, la végétation est faible, les filets sont peu nombreux, et par consequent la stipe est grêle. A mesure que l'arbre s'éleve, la végétation devient de plus en plus active, le nombre des filets augmente sensiblement, le stipe grossit. Mais quand l'arbre a atteint une certaine épaissure la végétation s'affaiblit, le nombre des filets diminue, le stipe va s'amincissant jusqu'au sommet."

Had M. Mirbel ever examined the trunk of one of these fusiform palms, or had he even read a description of their method of growth, he never would have tried to explain this increase in size in this manner.

I am not able to give at present the physiological reason for this peculiar growth, but I am able to give some explanation of how it occurs. In transections these palm stems show the same number of bundles in the swollen part as in the more slender parts both above and below it. When there is a difference, it is such as may be found in any palm having a cylindrical trunk. In the swollen part there is a great increase of cellular tissue, and a very slight increase in the size of a few of the fibro-vascular bundles. M. Mirbel represents this enlarging as taking place during the growth of the tree, and at the top; whereas it does not occur until the palm has attained almost its full growth. The *young Iriartea ventricosa* never shows this enlargement in any part of its stem, and when it does occur in the grown plant, it is at a considerable distance below the growing part.† In some species of *Acrocomia* the swelling takes place near the summit, but always after the crown of leaves or phylophore has passed the part. In one species examined at Asuncion, in Paraguay, the trunk has no certain point at which it swells, but may swell out either at the base or the summit, or anywhere between the two parts, and there are many cases in which there are swellings both at the base and just below the fronds. Neither is the tapering of a few palms like *Oreodoxa oleracea* and *Euterpe oleracea* to be explained by a decrease of the number of fibro-vascular bundles toward the top. In examining many trunks of *Euterpe,* I found the number of bundles near the base and near the top about the same, but I always found, where there was a decided tapering of the trunk from base to summit, that there was a difference in the size of the bundles, slight to be sure, but quite as marked as the difference in size of the two parts of the trunk. This difference in the size both of the trunk and of the bundles is more noticeable in *Oreodoxa oleracea*, or the royal palm, than in any other palm which came under my observation.

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* Comptes Rendus de l'Acad, 1843, II, p. 1123.

† Wallace's "Palms of the Amazon," p. 37.

I have spoken of the branching of the fibro-vascular bundles and their return always to a frond base, as if their course was on the same side of the trunk and in a vertical line. Neither is the case. It often happens that instead of returning to a frond base upon its own side, the bundle crosses through the whole stem and connects with one on the side opposite.* Mirbel claimed that in the date palm, the bundles all crossed from one side to the other. I shall not say this is not true of the date palm, for I am well aware that there is a great variation of structure among palms, but I have never found this crossing from side to side to be the rule, although it often occurs, and is more marked in some palms than in others.

In addition to this occasional crossing the stem, the bundles have a winding direction, so that their course is not directly vertical, but spiral, both right and left, about the stem, part of them going to one side and part to the other. From base to summit then, a bundle may be said to have a spiral plane within which it grows, and whether it returns to the surface upon the side on which it originated or upon the opposite side, it is always in this spiral plane. Meneghini tried to explain this spiral direction of the bundles as a mechanical result of the growth of the tree whereby the relative sizes of the trunk and frond bases became changed. He supposed the fronds upon the apex to be arranged in a helix, and that as the tree grew this helix developed into a spiral line upon the stem. He believed the leaf bases to be always of the same size, both upon the growing cone and upon the stem. The growth of the trunk then, and the unchanged size of the bases of the fronds necessitated a drawing of the bundles toward these bases, which resulted in the spiral direction.

But I have observed that the relative position of the fronds is always the same, a matter which Von Mohl was in doubt about. The spiral direction of the bundles is in no way a mechanical one, but exists alike in stem and phylophore as I have often observed, and until some better reason can be assigned for it, must be considered as organic.

The existence of a palm having its fronds arranged in one plane† would of itself be sufficient to upset Meneghini's theory of the helix and spiral. This spiral direction of the fibro-vascular bundles is an important one, both in connection with the structure of the plant, and in its influence upon the plant's general appearance.* It varies greatly in different species, and may be almost wanting. In trying to split palm stems, those in which the spiral direction is less marked, split more readily than those in which it is more decided. It is not very marked in *Mauritia caraná, Euterpe,* and *Iriartea,* while in *Maximiliana* and *Manicaria* it is a very prominent feature.

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* Dr. Von Martius believed this to be the case, as will be seen in the Comptes Rendus de l'Acad., 1845, Vol. I, p. 1038.

† About Pará and the mouth of the Amazon a distichous palm is very common. It is popularly known as the *baccába*, and is the *Œnocarpus baccaba* of Martius. *Urania speciosa* and *U. amazonica* are other distichous monocotyledons.

It is not in the trunk alone that spiral direction is to be seen, but it is more or less observable in the fronds and spathes. The trunk may have a very decided spiral direction in its fibro-vascular bundles, which may be wanting in the fronds, and *vice versâ*. *Raphia tædigera* (vulg. *Jupatý*), for example, has a marked spiral direction of its bundles in the trunk, while the petioles of the fronds split with almost perfect evenness. Spiral direction in spathes is well shown in the spathe of *Manicaria saccifera* (vulg. *Ubussú*), which resembles coarse cloth somewhat.

In the petioles and midribs of some palms, modifications of spiral direction give rise to peculiar and characteristic forms of midribs, resulting in changes of the leaf planes from a horizontal to a vertical position, which are characteristic of the species in which they occur.

It has been noticed by those who have studied and observed palms in their native forests, that, after a certain amount of experience in familiarizing one's self with the general appearace of them, the common palms can be distinguished at almost any distance at which they are visible, if only the fronds can be seen. In those having pinnate fronds this is very largely due to the effects produced by changes in the leaf planes, which are the result of changes in the shapes of the midribs, which, in their turn are the result of the direction of the fibro-vascular bundles. In the *Maximiliana regia* Mart. (vulg. *Inajá*) and *Attalea excelsa* (vulg. *Urucurý*) of the Amazon region, and in *Acurý*,† of the upper Paraguay, the bundles in the midrib are turned to one side as shown in figure X, page 477.

In No. 1 is shown a section across a midrib not far from the trunk, where it has the usual shape of a midrib. In No. 2, a section further outward, the bundles of the side CB (1) have moved up and gone to form an extension of AB, while a corresponding number from the side AC have taken their places on CB. The result is a figure like No. 2. No. 3 represents a section still further out, and No. 4 is one near the tip, this direction to one side being more marked the nearer we approach the end of the frond. The midrib assuming these forms, it is impossible for the frond to maintain its horizontal position, whereupon it changes its leaf plane from a horizontal to a vertical position, and droops over on its edge. It might be supposed that this twisting of the frond is due to some arrangement of the leaflets with reference to the light, but in the *Maximiliana regia* (*Inajá*) the tips of the fronds are completely inverted in a great many cases, if not always, so that what was originally the lower side of the frond is turned upwards.

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* I have not studied the relation of the spiral direction of these bundles to the phylotaxis, but I suggest that the two are related.

† Botanical name not known.

In a number of transections of a large, living and nearly grown palm stem, in those made near the base, it is found that the fibro-vascular bundles are all black, if black be the characteristic color of the mature bundles,* except a few in the centre. A section made anywhere below a certain distance from the fronds would show the same general character as regards hardness and color. But on coming near the growing part the sections appear less and less colored, and above the fully-matured frond's they are all found to be colorless. Dissecting out these bundles in the phylophore we find that those already colored, or nearly so, connect with the lower or more mature fronds, while those connecting with the younger fronds are, for the most part, colorless; and, when showing any color at all, it is only at the lower extremity of the division. We find, then, that there are uncolored bundles near the base of the trunk at the centre, and also all through the section near the top. I therefore place these facts against the theory of Mirbel, that the color of the bundles is due to age alone,† and also against that of Von Mohl, which is that color is due to position alone. In regard to this coloring, the element of age is a necessary one when the division is considered longitudinally, for in this case the bundle is colored for a short distance at the upper end where it passes in to the centre, then follows a part in which it is comparatively uncolored, while the remainder, and larger part, is colored. But in considering a transection of a trunk with reference to the coloring of the bundles, position is the necessary element. This is because the lower extremities of the divisions begin to color and harden before any other parts, and, as has already been explained, these lower extremities lie next the surface of the stem.‡

Thec omplete hardening and coloring of the fibro-vascular bundle divisions does not take place until the frond or spadix, with which they are connected at their upper extremities, have fallen or died. As has already been mentioned, the bundle divisions begin to harden and color at their lower extremities before the frond or spadix dies, but not before it is unfolded and active. At the fall or death§ of the frond the hardening and coloring are complete, and this marks the limit of growth of the division bundles originally connected with it. As far as these hard, colored bundles are concerned, the growth of the whole stem is at an end. In fact, however, the stem does continue to grow to a certain distance below the phylophore, but this growth is lateral and not longitudinal. A palm trunk may grow laterally as long as the fibro-vascular bundle divisions of the given part are in connection with active fronds.* It is plain, then, that there can be no longitudinal growth below the lowest active fronds. But in regard to lateral growth, there is no practical line of demarkation between the full-grown and growing parts of a trunk, because full-grown and growing parts overlap each other. Theoretically the growth has ceased below the lower extremity of the bundle divisions connected with the lowest active fronds. Practically it varies much with the species, age, vitality and circumstances of the individual.

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* Some palms have the mature fibro-vascular bundles of a waxy color, such as *Oreodoxa*, *Euterpe* and *Geonoma*; others have them of a deep, reddish-black, like *Mauritia*; while the majority of them are black. Examples: *Acrocomia, Guilielma, Astrocaryum, Bactris*, etc., etc.

† Ray Society, 1849, p. 82.

‡ The edible part of the "palmito" of Brazil and of the "cabbage palm" of the West Indies, is the long phylophore in which all the fibro-vascular bundles are soft and colorless.

§ I mention the falling *or* death of the frond because in some palms the fronds fall as soon as they die, while in others they cling to the trunk for a long time after death. Ex.: *Acrocomia lasiospatha*.

Being impossible below the fronds, longitudinal growth is necessarily confined to the phylophore or part above the lowest active frond. We may therefore naturally expect to find palms that have long phylophores attaining considerable heights, and having the internodes long. In almost all young palms, whatever the species, we find the phylophore very much longer than in full grown ones of the same kind, and the internodes longer in the same proportion. The young *Mauritia flexuosa* has its active fronds covering it down the trunk four or five times as far as an old individual of the same species, and the same is true of all the palms I can now call to mind. But this long phylophore gradually shortens with age, while the internodes shorten in the same proportion, and the fronds have a more decided drooping. In genus *Desmoncus* the trunk is covered with active fronds for a large part of its whole length, or, in other words, it is nearly all phylophore, and, as might be expected, we find it attaining enormous lengths,† with a very slender stem and long internodes, in comparison to its size. The length of the phylophore in this genus, as compared to its size, has caused it to assume the habit of a clambering or climbing palm. It reaches so great a length before any of its fronds cease to be active, that is, before any of its fibro-vascular bundles harden, that it is incapable of sustaining its own weight. If an *Assaí* (*Euterpe oleracea*) palm retained its fronds active to the same length proportionally that *Desmoncus* does, it would grow to be about a hundred feet long before its fibro-vascular bundles hardened near the base, and the result would be that it would fall over and become a clambering palm. The slender trunk alone of *Desmoncus* is not sufficient to account for its habit, for it falls over while it is still a mere shoot, not more than three or four feet in length. Then too there are many palms even more slender than *Desmoncus*, palms

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* Sachs (Text-Book, p. 552), says that "each portion of the stem, when once formed, maintains the thickness which it had already attained within the bud near the apex of the stem." There may be some palms of which this is nearly true, but it is far from being true in all cases, while it leaves the swelling of spindle-shaped trunks as badly accounted for as do the explanations of M. Mirbel.

† I have seen this palm over thirty metres long with a stem but little more than one centimetre in diameter.

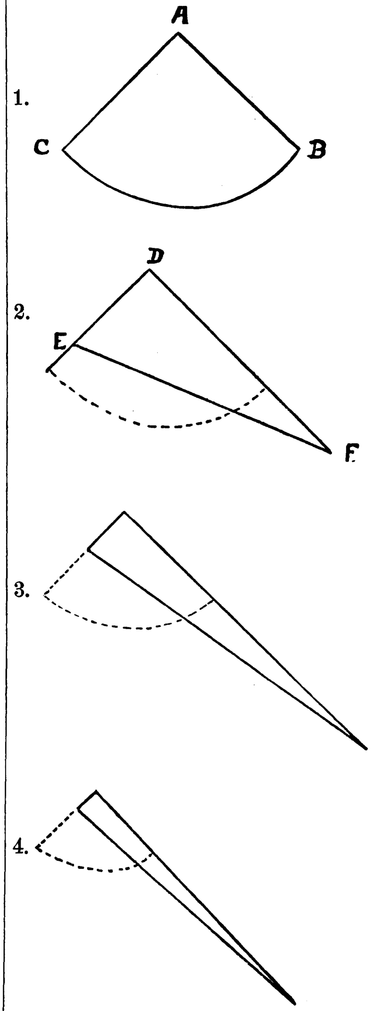

Fig. X.

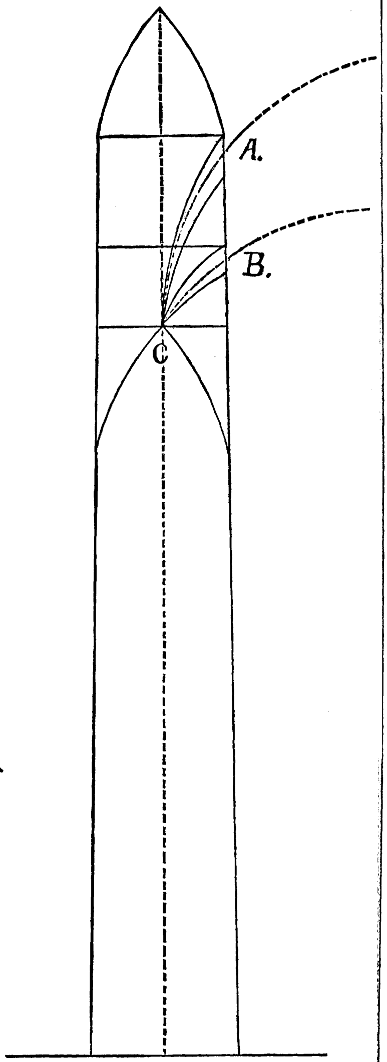

Fig. XI.

whose trunks are not larger than an ordinary lead pencil, but which, having the phylophore comparatively short, have the fibro-vascular bundles hardened early, and are consequently perfectly upright in habit.

I have not seen the Asiatic genus *Calimus* growing, nor have I been able to see any careful description of it, but judging from its slender stem and long internodes, I venture to guess that it has a very long phylophore, and to suggest that its great length and clambering habit is to be explained in this same manner.

Speaking of palms in general, in the same individual, the length of the internodes has much to do with giving it character as seen in its general appearance. As the length of the internodes, the age and vigor of the plant, and the drooping of the fronds are all intimately related, I will speak of these subjects in the same connection.

The drooping of fronds which is so much more marked in old palms than in young ones, in feeble than in vigorous ones of the same species, is caused :

First. By a decrease of the strength and vigor of the fibro-vascular bundles of the midrib. This variation in the strength of the midrib effects the drooping of the frond throughout its whole length.

Second. By the decrease of the vital powers of the whole plant, from which it results that the angle made by the outcurving bundles with the axis of the stem is larger than in the case of more vigorous growth.*

This effect can be seen by diagram, figure XI, in which C is the point of the phylophore where a frond is originated. In a case of feeble growth, the frond would stand out at B, making a large angle with the axis of the stem, while in case of vigorous growth, it would stand out at A, making a comparatively small angle with the axis. The result of difference in growth is very distinctly seen by comparing the young plants with old ones of the same species grown on the same soil. In the young ones the internodes are invariably† longer, and just as invariably the fronds are more erect. The fronds being continuations of the bundles, the angle made by the bundles with the side of the stem is continued into the fronds under slight modifications. The effect of this angle upon the fronds is also noticeable in the phylophore, for the angle at which the bundles cross the periphery being smaller in the cone-shaped apex, the fronds have a more nearly erect position. In figure XII, the upper fronds make a smaller

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* Hence the angle of drooping in fronds, taken alone, is not always a specific characteristic, as stated by Wallace in his "Palms of the Amazon," p. 5.

† Peculiar circumstances may change this, as I once saw well illustrated in the case of a *Mauritia flexuosa* near Pará. The whole trunk was about thirty metres high, and about six metres below the fronds, the old scars were very close together, and the trunk had every appearance of having completed its growth at that point. Above this, however, the trunk appeared to have renewed its youth, and the internodes were long and smooth like those of a vigorous palm. In seeking the possible explanation of this new growth, I found that the place where the palm stood had, a great many years before, been a forest, and that it had originally stood in the edge of a stagnant pool which had been drained. Whether these were the causes of the renewed vitality there were no means of ascertaining, but the evidence of that vitality was unquestionable.

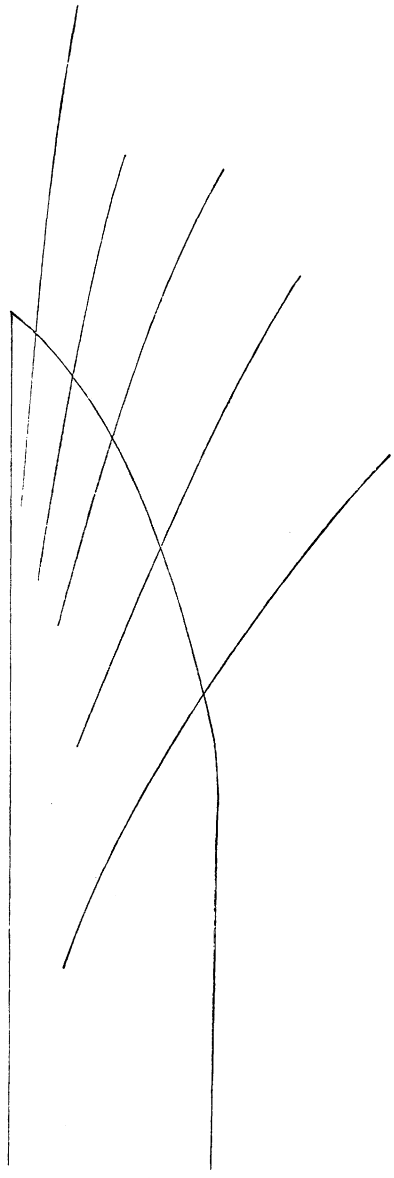

FIG. XII.

angle with the surface of the apex, and are more nearly erect. But when, in the course of time, the fronds which are now the highest, come to be the lowest, the angle they make with the periphery will have been much increased by the lateral growth of the trunk, which will bring the fronds out at shorter radii, and the result will be a more decided drooping of the lower fronds. In this arrangement upon the growing part is a provision for the weakness of the young fronds, which could not sustain their own weight if the angle made with the trunk were a larger one. I have already explained that the shorter radius at the surface, as seen in the lower fronds, is due to the lateral growth being greater than the longitudinal, and, of course, takes place as the fronds come to be the lowest in the crown.

I have also stated that in palms having perfectly cylindrical stems, the fibro-vascular bundles *average* the same size from the base to the upper end of the full grown part. They vary however in each division, reaching their greatest development within the trunk just where they curve outwards to connect with the external growth, and beyond this to a distance in the petiole varying with the length and weight of the normal frond. The variation in size appears to be due to the purpose which the bundle serves at the given part. In those palms which have long and heavy fronds, the bundles are greatly developed near the base, and in addition, they assume structural forms capable of adding to their strength in the manner needed by the tree, while in those having short and light fronds there is comparatively little development of the bundles at the bases of the petioles.* The frond of *Raphia tædigera* (*Jupatý*) is noted for its great length and weight.† In this palm the fibro-vascular bundles are cylindrical, or reach their greatest lateral development just at the juncture of the frond with the stem, and are flattened laterally in the base of the petiole, the upper edge being the thicker. This shape gives them about three times the strength they would have in the ordinary cylindrical shape, for supporting a weight applied as it is in this part of the petiole. There is another structural peculiarity about these bundles in *Raphia tædigera*, which I have not sufficiently investigated. When a frond dies, it breaks off just beyond the enlarged part of these bundles, and in time the broken petiole that remains fast to the trunk decays, leaving the larger fibro-vascular bundles exposed. In this condition, one might expect to find them bent downwards by the strain of great weight sustained by them from the beginning until they became rigid. But so far are they from being warped downwards, they are not even straight, but bend back in exactly the opposite direction to that given them by the drooping of the frond.*

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* *Jupatý*, *patauá*, *murumurú*, *urucurý* and *uauassú* all have large fronds, and proportionately large fibro-vascular bundles in the bases of the petioles. *Assaí*, the *marajás*, the *paxiúbas* and *mucajás* have small fronds, and small bundles in the bases of their petioles.

† I have measured fronds of this palm that were fifteen metres long. Wallace says he has seen them fifty feet long. V. Wallace's "Palms of the Amazon," p. 43.

Gaudichaud maintained that the fibro-vescular bundles of the palm-trunk ran down into the roots. My own observations agree with those of Von Mohl, that there is no such direct connection between the bundles of the stem and those of the roots. Anyone acquainted with the habits of such a palm as *Iriartea exorrhiza* could never have conceived a theory so out of keeping with the facts of the case. This palm puts out new roots continually, as do almost all palms, and always above the older ones. If the bundles of the trunk ran directly into the roots, the same roots would have to serve the tree through its whole lifetime, for the number of bundles in the trunk does not increase. To be sure, Gaudichaud maintained that the bundles descended from the fronds to the roots, and granting his premises there might have appeared to be some reason in this conclusion. But the supposition that the bundles ran downwards necessitates, as a consequence, a base much larger than the upper part of the trunk, as well as a continually increasing one, or else very small bundles at the base. None of these things are found to be so, but it is found that the bundles of the trunk do not run into the roots.

Von Mohl considers the spines on the aërial roots of *Iriartea exorrhiza* to be aborted rootlets, and directly connected with the fibro-vascular bundles of the roots. I also found them to be aborted rootlets, but they are as independent of direct connection with the bundles of the roots proper, as are the roots themselves of the bundles of the trunk.

In conclusion I find : (1) that all fronds and spadices originate at the centre of the phylophore ; (2) that the fibro-vascular bundle division continues to grow until its frond reaches maturity ; (3) that the growth of a palm trunk continues as long as the bundle divisions of the part are in active connection with living fronds, and no longer ; and (4) that the growth of palms is therefore an internal growth, and the term endogen is not a misnomer as far as palms are concerned.

From another point of view I find, that the outward appearance of a palm, the form of its trunk, the plume-like drooping of its fronds, the motion given them by the wind, the breaking and twirling of its leaflets, and its general picturesque beauty are only the outward manifestations of the laws of its internal growth and structure.

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* Another interesting point in regard to the bundles in the fronds is the direction in which they face. (For want of a better definition I have spoken of the side of the bundle connecting with the parenchymous system as the face.) I have not made a sufficient number of observations to enable me to speak authoritatively upon the subject, but in the few instances in which I observed this facing of the bundles, they tended to face the centre in the petiole and midrib just as they did in the trunk. In order to assume this position the bundles in the lower side of a frond retain the position they have on leaving the trunk, while the upper ones twist one way or another in what seems an endeavor to turn over and face the centre of the new stem—that is, of the petiole.

Note :—The preceding discussion is based upon direct personal observation and study of a large number of specimens of the following genera, together with others, the botanical names of which I do not at present know :

Acrocomia,
Attalea,
Astrocaryum,
Bactris,
Copernicia,
Cocos,
Desmoncus,
Euterpe,
Geonoma,
Guilielma,
Hyospathe,
Iriartea,
Mauritia,
Maximiliana,
Œnocarpus,
Oreodoxa,
Raphia.

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If, however, any should prefer to relegate it to a system of "passage-beds" connecting the Onondaga and the Lower Helderberg, no valid objection can be raised to the course pending the discovery of further and conclusive evidence. It will not affect the arrangement above proposed.

I must remark in conclusion, that the suggestions now made are provisional, and therefore subject to change, according to future evidence. It does not seem probable, however, that the main outline of the plan will be altered.

Note. Since this paper was written I have obtained an excellent specimen of *Pterygotus Osborni,* Hall, from the massive limestone of Juniata county. This may be considered a proof of the identity of this limestone with the *Water lime* of New York. For this specimen I am indebted to Mr. Jas. Stevenson of this city (Akron, O.), a former resident of Juniata county, Pa.

SUMMARY OF THE GROUPING DETAILED ABOVE.

	New York.	*Perry County, Pa.*
Lower Helderberg Gr.	Upper Pentamerus limestone.	
	Encrinital limestone.	Flint shale with Crinoids.
	Delthyris shaly limestone.	Lime shales with *Tentaculites, Meristella,* &c.
	Lower Pentamerus limestone.	
	Water lime (Tentaculite bed).	Massive limestone with *Pterygotus* and *Lep. alta.*
Onondaga Gr.	Magnesian rock.	
	Vermicular rock.	
	Gypseous marls.	Gray, calcareous shale.
	Variegated shale.	Variegated shale.
	Red Shale.	Red shale.
		Passage-beds.
Clinton Group.	Limestone.	Limestone and hæmatite.
		Sandrock.
	Iron ore.	Hæmatite.
		Sandrock.
	Upper green shale.	Upper green shale and fossil ore.
	Iron ore and limestone.	Iron sandstone and fossil ore.
	Lower green shale.	Lower green shale.
	Medina sandstone.	

ERRATUM.

In Mr. Branner's paper on the growth of the Palm, for *Guilland,* read *Guillaud;* and for *Ser. VI, 176, 1877,* read, *Ser. V, 1—176 1877.*